NASA-TM-112333

NN-52-TM
028918

Reprint from Symposia of the Swedish Nutrition Foundation V

EXERCISE AND WATER-ELECTROLYTE BALANCE

by John Edward Greenleaf[1]

Introduction

After oxygen, water becomes of prime importance for maintaining the health and well being of the human organism. Healthy people can live 3 to 4 weeks without food but less than 18 days without water (Wolf, 1958); the exact time depends upon the rate of the negative water balance. Physical exercise exerts a powerful influence upon the dynamic body-fluid and electrolyte equilibrium. In most circumstances exercise is associated with an increase in body temperature and the effects of the various degrees of heating must be considered when fluid and electrolyte shifts are discussed. If sweating occurs and the water and electrolytes are not adequately replaced—a common occurrence—the compensatory reactions to water depletion must be added to those of heat in determining the mechanisms involved in the maintenance of fluid-electrolyte homeostasis during exercise. In this review the term exercise refers to the movement of the body in the upright position. The profound effects of immobilization, changes in body position, and simulated weightlessness on water and electrolyte balance are beyond the scope of this paper: there has been a renewed interest in these three areas by workers in space medicine and nutrition.

There are large gaps in our knowledge of the nutritional aspects of water and electrolyte balance associated with various levels of physical exercise in normal healthy people. I will attempt to briefly summarize the normal water and electrolyte distribution, followed by a discussion of the effects, singly and in combination, of exercise, heat, and hypohydration on the water and electrolyte balance in general, the resultant changes in circulatory and renal functions, and the subsequent effects on thirst and drinking in particular. The effects of water depletion upon physical performance will also be discussed with some practical remedial suggestions. The term hypohydration refers to the state of diminished water content in the body; normohydration to the normal, *ad libitum* water balance; and hyperhydration to an increase in water content above normal.

Normal Distribution of Water and Electrolyses

The volume of body water is normally regulated to within ± 0.22 per cent of the body weight and voluntary drinking is usually stimulated when the body water decreases about 1 per cent (Wolf, 1958). The turnover of total body water has been estimated between 11 and 13 days (Hardy and Drabkin, 1952; Schloerb *et al.*, 1950). A typical daily water balance is presented in Table 1. These figures can be drastically changed if the body is subjected to heat, exercise, altitude, starvation and so forth. The average volumes of the classical fluid

[1] National Aeronautics and Space Administration, Ames Research Center, Moffett Field, California, U.S.A. *Present address:* Department of Physiology, College of Physical Education, Stockholm, Sweden.

TABLE 1. *Typical daily water balance in man:*

Source	Weight, g
Input	
Beverage	268
Food moisture	2018
Water of oxidation	254
Preformed	33
Total	2573
Output	
Urine water	1482
Fecal water	105
Insensible water	1102
Sweat	0
Total	2689
Water balance (input–output)—116	

From R. E. Johnson. Conference on Nutrition in Space and Related Waste Problems. NASA SP-70, 1964, p. 166.

spaces in ten men indicates there are about 39 liters of water in a 72.5 kg man that constitute about 54 per cent of the body weight (Table 2). These figures are subject to some variation depending upon the methods used for measurement. Also, the greater the percentage of body fat the lower will be the per cent of total body water based upon total body weight because fat contains much less water than "lean body mass". It should be remembered that these various "compartments" are only convenient models of the fluid distribution system and must be interpreted as such. However, the compartment concept has proven extremely useful in elucidating the mechanisms of fluid distribution and for the treatment of various disease conditions.

TABLE 2. *Fluid spaces in 72.5 kg man.*[a]

Space	Per cent body weight	Liters per man
Extracellular→	23	17
Plasma	4	3
Interstitial	19	14
Intracellular→	31	22
Total	54	39

From F. D. Moore *et al.* The Body Cell Mass and its Supporting Environment. Philadelphia: Saunders, 1963, p. 532.
[a] Average of ten men ages 23–54.

Sodium is the major cation and chloride the major anion in the extracellular fluid (Table 3). Thus, changes in the sodium concentration indicate, approximately, changes in extracellular fluid (ECF) volume. Potassium is the major intracellular (ICF) cation and phosphates and protein the major ICF anions. Even though there is a rather large difference between the ICF cation and anion osmolarity (175 and 135 = 310 mOsm/l) the total ICF osmolarity is exactly equal to the total ECF osmolarity (155 and 155 = 310 mOsm/l). Thus, essentially equal osmotic concentration is maintained between two fluids of widely different ionic composition.

That the fluid composition of the mammalian organism is maintained according to the laws of osmotic pressure was shown by Darrow and Yannet (1935). By increasing and decreasing extracellular electrolytes while holding total body water (TBW) relatively constant they concluded: 1) Osmotic equilibrium exists between cells and water; 2) Nine-tenths of the body's osmotic pressure is maintained by electrolytes; 3) Sodium and potassium roughly determine water distribution; 4) Osmotic equilibrium between the plasma and red blood cells (RBC) is achieved mainly by the transfer of water; and 5) Marked changes in TBW distribution can occur even when the TBW volume is essentially unchanged.

The role of the fixed base (Na^+, K^+, Ca^{++}, and Mg^{++}) in controlling water distribution was further emphasized by Lavietes *et al.* (1935). Small changes in base concentration, particularly if the base

TABLE 3. *Normal composition of fluid spaces in man.*

Space	Cations				Anions			
	NA+ mEq/*l*	K+ mEq/*l*	Other+ (Ca + Mg) mEq/*l*	Osmols+ mOsm/*l*	Cl− mEq/*l*	HCO_3^- mEq/*l*	Other− (PO_4 + PRO mEq/*l*	Os-mols− mOsm/*l*
Extracellular	142	5	8	155	103	27	25	155
Intracellular	10	145	20	175	2	8	190	135
Total	152	150	28	330	105	35	215	290

From J. L. Gamble. Extracellular Fluid. Cambridge: Harvard Univ. Press, 1960.

has a high concentration, would exert significant changes on water distribution. For example, a change in 2 mEq of a base whose original concentration was 150 mEq/l in a total volume of 50 liters would account for $50 \times 2/150 = 0.67$ liters of water. They concluded that: 1) The concentration of total base is approximately equal throughout all of the TBW; 2) A change in the concentration of any one portion is equalled in all other portions; and 3) The ECF, ICF, and blood volumes may vary independently of one another. These conclusions must be addended to the effect that a sufficient amount of time must be allowed for equilibrium to take place. In short term studies on dogs, forced administration of large amounts of water produced demonstrable changes in the volume and electrolyte distribution in the blood greater than that expected from the degree of dilution (Greene and Rowntree, 1921). Conversely, in studies of chronic administration of water in normal men with sufficient time allowed for equilibrium to take place, daily water intakes up to 9,570 ml did not alter serum osmolality and the latter was not significantly different from control values (Habener *et al.*, 1964).

The importance of the kidneys in the regulation of volume and solute concentrations has been known for many years, but they can correct only for an excess of fluid. If body water is depleted the kidneys will concentrate the urine to about 1400 mOsm/l and continue to do so until they fail or until water is ingested. Thus, during hypohydration the water intake mechanisms become of prime importance. The condition of involuntary hypohydration, where voluntary water intake lags considerably behind water losses, occurs in most mammals but is most pronounced in man.

To define some of the metabolic variables associated with normal voluntary water consumption, data from 87 basic trainees, living in a hot-moist environment, were analyzed utilizing a stepwise linear regression statistical analysis (Greenleaf *et al.*, 1966). Twenty-two variables were examined and six variables (1) mean daily urinary volume, (2) serum osmolarity, (3) lying pulse rate, (4) mean daily urinary Cl, (5) mean daily urinary K and (6) rate of sweating accounted for 62 per cent of the variation in water intake (Fig. 1). The addition of the other 16 variables accounted for only 71 per cent of the variation. An estimation equation was constructed from the 6 variables and a plot of the estimated versus the measured water intake is shown in Fig. 1. The multiple correlation was 0.787 and the standard deviation ± 575.74

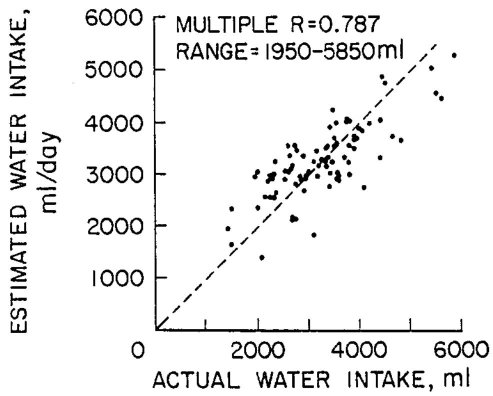

Fig. 1. Estimated versus actual water intake (87 subjects). The estimated water intake was calculated from the equation. From Greenleaf, Averkin, and Sargent (1966 *c*).

$\bar{y}$ water intake (ml/day) =
− 11,502.40 + 45.81 (serum osmolarity, mOsm/l),
+ 1.1524 (mean daily urinary vol., ml/day),
− 18.86 (mean daily urinary K, mEq/day),
+ 4.3881 (mean daily urinary Cl, mEq/day),
+ 1.7671 (rate of sweating, ml/hr),
− 18.72 (lying pulse rate, beats/min).

ml. Since volume and concentration variables are included among the six, it seems apparent that some combination of body osmolarity and body fluid volume is closely related to voluntary water intake in man.

Exercise and Water-Electrolyte Balance

The literature on the relationships between exercise and body fluids up to 1960 has been extensively reviewed by Moore and Buskirk (1960). Acute exercise (up to 1 hr. duration) first effects a decrease in plasma volume which then gradually returns to or slightly below initial levels unless hypohydration intervenes (Åstrand and Saltin, 1964; Jarošová and Daum, 1951). In prolonged exertion plasma volume may exceed control values (Åstrand and Saltin, 1964); this elevation may be an example of the over-shoot phenomenon common to feed-back systems. However, the subjects had been drinking water during the exercise period and some of it could have been resorbed from the intestines into the extracellular space. The efflux of plasma fluid is apparently assimilated by the interstitial fluid to help balance the increased ICF osmotic pressure created by the active muscle cells with little change in the total volume of the ECF (DeLanne *et al.*, 1958 and Kronfeld *et al.*, 1958). Kozlowski and Saltin (1964) found the ECF volume was maintained at the expense of the ICF volume during hard work at 18°C; the ECF (inulin space) decreased 1.2 per cent, the plasma volume (Evans blue space) decreased 1.5 per cent, but the ICF (TBW minus ECF) decreased 8.4 per cent: and the plasma K concentration rose to 5.6 mEq/l at the end of the exercise. The difference between the reduction in fluid spaces after thermal and exercise hypohydration can be explained by the fact that the water associated with the glycogen would be free for use during the exercise experiment. Åstrand and Saltin (1964) also observed an increase in plasma K to 5.3 mEq/l (29%) 1 hr. after an 85-km cross-country skiing race while the Na and Cl concentrations were essentially unchanged. Kjellmer (1961) has found a correlation between the increase in venous K and exercise hyperaemia. Since little protein (about 1%) is lost from the vascular system during exercise (Keys and Taylor, 1935), the majority of the fluid loss must be the result of hydrostatic pressure differences caused by the exercise (Kaltreider and Meneely, 1940; DeLanne *et al.*, 1958). However, the concentration of plasma proteins increases due to hemoconcentration and the ratio of albumins to globulins increases in the early stages of work; there is a transfer of proteins from the general circulation to the intercellular spaces during exercise; and, as work progresses or ceases the plasma protein concentration returns nearly to normal values (DeLanne *et al.*, 1958).

Renal blood flow reflects the decreased blood volume and may decrease by 50 per cent depending upon the intensity of the exercise and the glomerular filtration rate falls in proportion to renal blood flow when changes in the latter are large. Sodium chloride, urea, creatinine, and phosphate excretion are decreased, probably due to the decreased glomerular filtration (Wesson, 1960).

The inhibition of urinary excretion, the net result of a decreased glomerular filtration rate and anti-diuretic hormone activity, usually does not occur unless the exercise is hard and then the flow diminishes rapidly and remains low until exercise ceases but rapidly returns to normal values (Wesson, 1960). Thus, the decrease in flow is not proportional to the intensity of the exercise.

If the effect of heat and/or hypohydration are superimposed upon those of exercise the mechanisms involved become more difficult to separate. Saltin (1964 *a*, 1964 *b*) and Saltin and Stenberg (1964) have conducted a series of acute experiments combining those three variables and the results concerning cardiovascular dynamics and water-electrolyte changes may be summarized as follows:

1. Hypohydration by heat decreased plasma volume and ECF ten times more than if the same degree of body weight loss was induced by exercise hypohydration. Thus, heat exerts its effects on the ECF volume while exercise predominantly depletes the ICF volume.
2. At submaximal work in the upright position there was a more marked heart rate increase after exercise than after thermal hypohydration. The stroke volume was decreased in both conditions.
3. During maximal work after either thermal or exercise hypohydration maximal heart rates and oxygen uptakes were unchanged from normohydration values.

The problem of voluntary consumption of water becomes important for water balance in men working in the heat for there is a considerable delay in rehydration following water loss (Hunt, 1912; Vernon and Warner, 1932). This condition has been termed voluntary dehydration (Rothstein *et al.*, 1947) or involuntary hypohydration (Greenleaf, 1966 *a*). The effects singly and in combination of heat (49°C) and cool (24°C): exercise (6.4 km/hr on a level, motor-driven treadmill) and resting (sitting): and hypohydration (4% of the body weight) and normohydration on voluntary water intake and water balance have been studied in four well-trained acclimatized young men (Greenleaf and Sargent, 1965). A weight sustaining diet consisting of sustagen (Mead–Johnson), saltine crackers, oleomargarine, and 14 grams of NaCl/day was eaten for 4 days prior to and also on the test day: $^1/_3$ of it during the pre-period, $^1/_3$ about hour 5 and $^1/_3$ about hour 8 (Fig. 2). In the 4 hypohydration experiments, water was restricted to 900 ml/day, and in the four normohydration experiments water was allowed *ad libitum*. The test day consisted of a 4-hr experimental period in an environmental chamber followed by an 8-hr recovery period at 24°C dry bulb temperature and 50% relative humidity when the subjects engaged in light, sedentary activity. The combination of increased NaCl intake and restricted water produced intense thirst. Tap water (24±5°C) was allowed *ad libitum* from

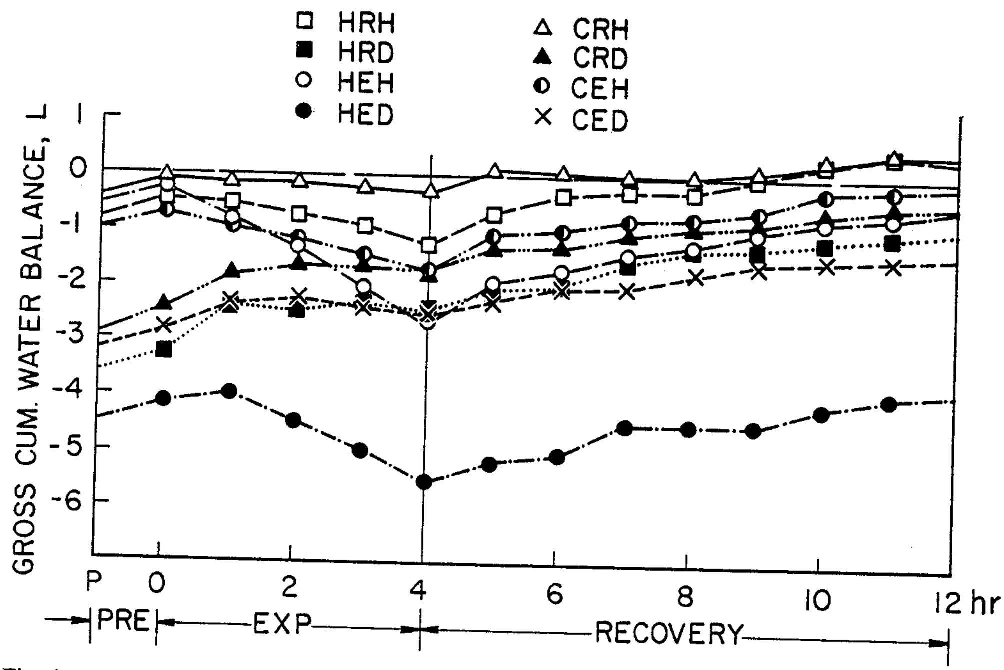

Fig. 2. Gross cumulative water balance in four subjects during the eight experiments. The water balance was calculated from changes in body weight corrected for water intake and sweat loss during the experimental period and water, food, and urine during the recovery period. Point P was the change in body weight from the first diet day. From Greenleaf and Sargent (1965).

the time the subjects entered the chamber until the end of the recovery period. The average water intakes during the experimental periods (Table 4) indicated that hypohydration and exercise were less effective than heat in stimulating drinking. Or, conversely, exercise was slightly more effective in inhibiting water consumption followed by hypohydration and heat. The recovery rates of drinking were quite consistent. The gross cumulative water balance also indicates the constancy of the recovery drinking (Fig. 2). Curve HED (heat, exercise, hypohydration) is of particular interest since the water balance showed no gain at the end of the recovery period compared with the beginning of the experimental period. One conclusion from these observations is when the diet is held constant the rate of repayment of a water debt is independent of the degree of water loss.

The total water consumption during the eight experiments (Fig. 3) indicates that drinking was directly proportional to the severity of the experimental conditions, i.e., CRH was the most difficult experiment while CHR was the easiest. The control

TABLE 4. *Voluntary water intake during the experimental and recovery periods (ml/hr).*

	Experimental		Recovery	
	Mean ±S.E.	Ratio	Mean ±S.E.	Ratio
Heat	629±108	*2.5*	254±16	*1.3*
Cool	256± 97	1	198±15	1
Exercise	518±134	*1.4*	244±22	*1.2*
Resting	367±150	1	208±18	1
Hypohydration	598±120	*2.1*	212±18	*0.9*
Normohydration	286±116	1	240±27	1

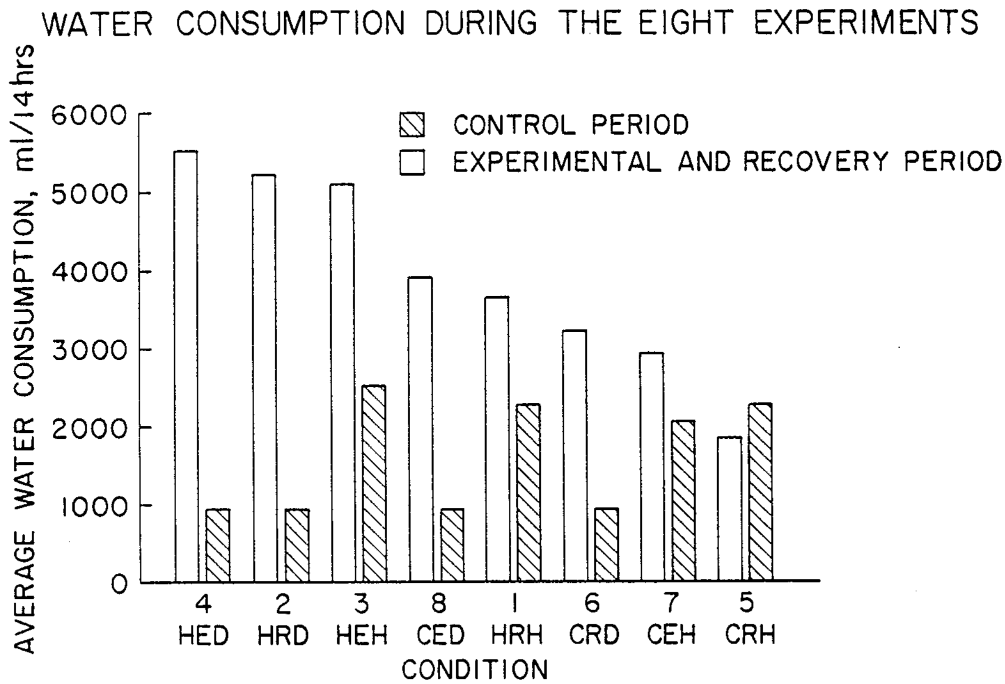

Fig. 3. Average water consumption in four subjects during the eight experiments. The control period is the average of the four dietary days. The pre-period, experimental, and recovery periods encompassed about 14 hours. From Greenleaf (1966 *b*).

period refers to the 4-day dietary period. Thus, water consumption is related more with the severity of the total stress than with the degree of water deficit (Greenleaf, 1966 *b*). Subsequently, the heat, exercise, hypohydration experiment was repeated to determine the effects of artificial heat acclimatization on involuntary hypohydration. During the exercise and recovery periods (Fig. 4) there was no difference in water balance between control and acclimatization experiments and negative water balances (−600 ml/hr) were present during the period of exercise in the heat. The return of body weight to normal pre-hypohydration levels required 48 to 72 hours. In the acclimatization experiment water intake dropped from 16 ml/hr-kg in the 2-hr exercise period to 4 ml/hr-kg after 2 hours of recovery (hour 4). The respective control values were 8 ml/hr-kg and 4 ml/hr-kg. By hr-4 the serum osmolarity in both control and acclimatized experiments had returned to normal (circa 283 mOsm/l). The calculated ECF balance (Fig. 5) indicates the difference between the volume of water needed to return the ECF osmolarity to 283 mOsm/l and the water actually consumed. The ECF volume was calculated as 66.9 kg $\times$ 0.234 = 15.655 liters. The cumulative ECF balance is indicated by the solid and dash lines. Within two hours after exercise a sufficient amount of fluid was assimilated by the ECF to return the osmolarity to 283 mOsm/l. During the recovery period (hrs 3 to 23) there was no sweat loss and the urinary flows averaged about 0.5 ml/min or a total loss of about 600 ml. Plasma volume (Evans blue space) was unchanged from baseline control values

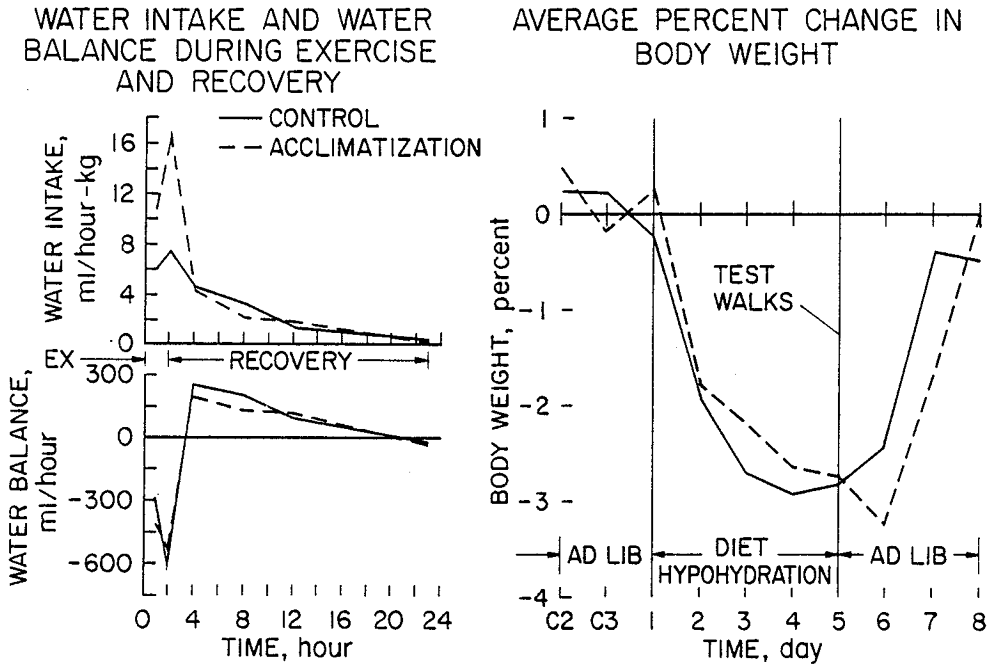

Fig. 4. (Left half): Water intake and water balance during exercise and recovery in four subjects. (Right half): Average per cent change in body weight during the control period (C2, C3), the dietary period, and the recovery period (days 6 to 8).

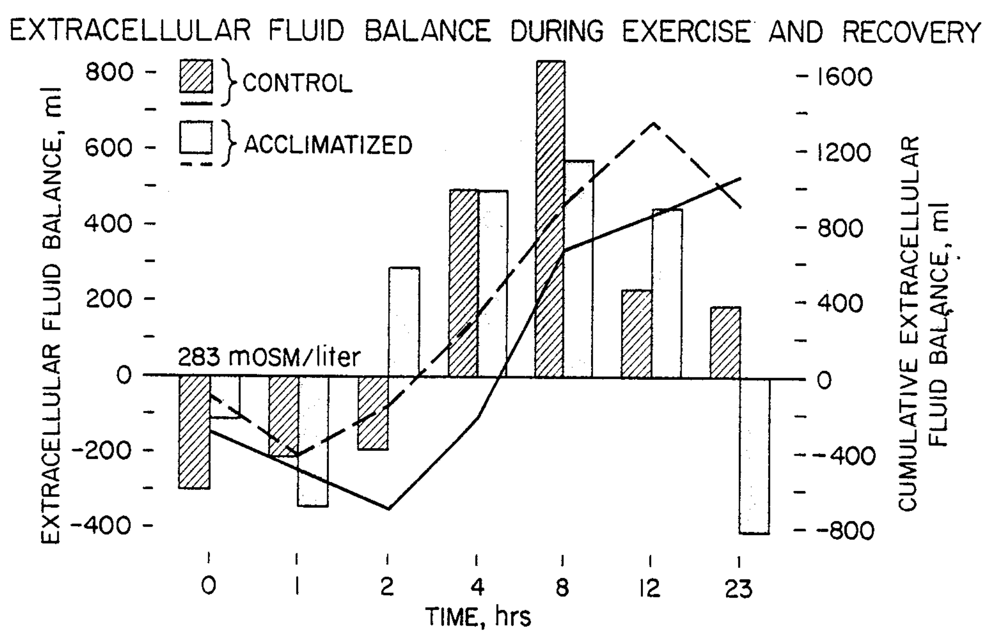

Fig. 5. Calculated extracellular and cumulative extracellular fluid balance in four subjects during exercise and recovery. Note the different ordinate scales.

1 hr after the exercise: Control baseline 2844 $\pm$ S.E. 200.0 ml, post-walk 2776 $\pm$ 78.5; acclimatized baseline 2882 $\pm$ 194.0, post-walk 2825 $\pm$ 112.5. Since serum osmolarity was essentially constant from hours 4 to 12 (it varied from 282.9 $\pm$ S.E. 2.0 mOsm/l to 285.9 $\pm$ 1.9) the non-urinary volume of water contributing to the positive ECF balance must have been assimilated into the intracellular compartment. If this is true, it would appear that under these circumstances ingested water is primarily utilized to regulate ECF tonicity with the ICF debt repaid more slowly. Thus, drinking virtually ceased when serum osmolarity returned to normal values in spite of the fact there was a weight deficit of about 3 per cent.

Effects of Hypohydration on Physical Performance

Water depletion occurs whenever exercise is performed. Within 2 seconds after heavy muscular work is initiated, sweating begins (van Beaumont and Bullard, 1963) and its duration and intensity is dependent on the work load, ambient temperature and pressure, and perhaps on the level of bodily hydration. Exercise also increases pulmonary ventilation, another avenue of water loss (with a ventilation of 8 l/min the water loss can vary between 12 and 18 g/hr depending upon the water content of the inspired air). The degree of physical deterioration is usually determined by acutely depleting the body water (expressed as a percentage of body weight) utilizing heat (Saltin, 1964 *b*; Craig and Cummings, 1966), exercise (Åstrand *et al.*, 1963; Åstrand and Saltin, 1964), a combination of the two (Saltin, 1964 *a*; Greenleaf *et al.*, 1967), or by chronically restricting water consumption and then comparing various physiological variables with a control group (Greenleaf *et al.*, 1966 *d*). In the acute experiments food and water are usually withheld until the experiments have been completed. In the chronic experiments caloric restriction introduces another variable accentuating water loss (Henschel *et al.*, 1953).

There is no gross impairment in physiological functioning with a body weight loss of 4 to 5 per cent in men in good physical condition (Greenleaf *et al.*, 1966 *d*; Kuno, 1956; Ladell, 1955) and at least to 3.3 per cent in well-trained women (Greenleaf *et al.*, 1967). However, the work capacity (work time on a maximal work load) was significantly reduced after hypohydration, particularly exercise hypohydration (Saltin, 1964 *a*, 1964 *b*). Well-trained subjects can work longer than untrained subjects (Buskirk *et al.*, 1958; Saltin, 1964 *c*). Mechanical efficiency and aerobic work capacity are unchanged (Saltin, 1964 *c*). When work is done in the upright position the pulse rate, blood pressure, and rectal temperature increases are exaggerated and orthostatic tolerance is reduced (Eichna *et al.*, 1945; Judy and Greenleaf, 1966). The cardiovascular responses show less response to hypohydration when exercise is performed in the supine position (Saltin, 1964 *b*). It has been well established that administration of water approximately equal to sweat loss results in improved work performance (Pitts *et al.*, 1944; Smith *et al.*, 1952) and pulse rates, blood pressures, stroke volumes and ECF volumes are maintained nearer normal ranges. Since saline solutions are retained in the body longer than plain water it would seem advisable to give salt, but there are divergent opinions whether NaCl should be given. Adolph (1946) and Pitts *et al.* (1944) cautioned against salt taken during short heat-exercise exposures, and others to the contrary (Ilzhöfer and Brack, 1932; Robinson, 1963). Ladell (1955) has demonstrated, on the basis of calculated changes in the ICF volume, that higher heart rates and rectal temperatures and lower sweat rates (indices of bodily deterioration) tended to be positively correlated with decreased ICF volumes. Since any salt in excess of losses would rapidly deplete ICF volume, he concluded that the best condition is achieved if water is taken in excess in relation to salt as the hypotonicity tends to maintain the ICF volume. It was concluded that exercise tolerance is better maintained by drinking water or saline than by not drinking or taking salt alone.

Hyperhydration of about 2 liters before exercise resulted in significantly lower pulse rates and rectal temperatures and higher sweat rates in men walking for 90 minutes at 5.6 km/hr at 49°C. However, the problem of muscle cramps appears if the body salts become sufficiently diluted. If fluids are forced during strenuous exercise, absorption is delayed because there is a delay in stomach emptying and the water does not pass on to the intestine (Greenleaf and Sargent, 1965). Intense emotional situations also delay gastric emptying. The composition of the rehydration fluid seems critical, particularly if drinking is ad libitum (Greenleaf, 1966 *a*). The conditions that tend to maintain good physical performance during negative water balance may be summarized as follows:

1. A high level of physical fitness for endurance activities.
2. Heat acclimatization.
3. Reduce the metabolic heat load to a minimum if work is to be performed in the heat.
4. The supine position is preferable when working in the heat.
5. During continuous work it is better to allow 20 to 30 minute rest periods every 2 to 3 hours than 10 min each hour.
6. Reduce the total stress and sweat loss to a minimum. The more water lost the longer the time needed for complete replacement.
7. Water intake equal to sweat loss and slightly more if possible. Plain water and fruit-flavored drinks are usually preferred in the temperature range 10–13°C with the optimal pH approximately 6.0. Always consider ethnic origin and normal drinking habits when prescribing fluids.
8. Salt intake to equal losses: if in doubt omit the salt if an adequate diet is available. Do not miss meals as drinking is directly related to food consumption.
9. Have the water supplies easily accessible: men would rather be thirsty than walk for a drink.
10. Drink small quantities frequently rather than large quantities infrequently.
11. Avoid high protein diets as this can lead to excessive urinary losses of water.
12. If water is limited drink nothing, if possible, for the first 24 hours to allow urine flow to reach minimum levels.

Summary

Physical exercise exerts a powerful influence on the dynamic body-fluid and electrolyte equilibrium. During normal daily activities voluntary drinking is usually stimulated when the body water decreases about 1 per cent and the latter is normally regulated to within ± 0.22 per cent of the

body weight. The turnover of total body water has been estimated at between 11 and 13 days. The water content tends to be distributed according to the laws of osmotic pressure and the composition of the various fluid compartments and the total body osmolality is maintained within rather narrow limits.

In general, when exercise commences, the fluid regulatory mechanisms allow fluid to be transferred to the working muscle cells. Plasma volume is decreased and this fluid moves into the interstitial spaces. The effective renal plasma flow is reduced in proportion to the severity of the exercise and the filtration rate is also reduced when the renal blood flow changes are large. Urine volume is decreased due to the reduced glomerular filtration and increased activity of the antidiuretic hormone. With the reduction in renal flow more water is available for sweat production if needed. While the circulatory and renal adjustments seem well-regulated to meet the demands of the exercise and the resulting heat load, the water intake mechanisms are not. Under stressful circumstances causing a deficit of body water, full replacement of water does not occur until some time has passed—often up to 72 hours. This delay in complete rehydration following loss has been termed involuntary hypohydration (or voluntary dehydration). In general, mild physical exercise (walking) inhibits voluntary water consumption more than high environmental temperature (49°C) or previous hypohydration (3 to 4% of the body weight). Following these various stressful exposures, the rates of rehydration are the same and independent of the water debt. Heat acclimatized subjects have greater water intake than non-acclimatized subjects. However, the greater sweat losses after acclimatization are balanced by the greater intake and there is no net gain in the overall water balance. Men exercising in the heat usually drink at a rate of $^1/_2$ to $^2/_3$ of the amount of water lost in sweat and urine. Water administered to equal or exceed sweat losses reduces physiological strain and increases work performance. For the most part, physical performance of men and women in good physical condition does not deteriorate appreciably until the water debt reaches 3 per cent of the body weight and the range can be extended to 4–5 per cent in men in excellent physical condition.

References

Adolph, E. F. (1946). *U.S. Public Health Reports Supp. No. 192.*

Åstrand, P.-O., Hallbäck, I., Hedman, R. and Saltin, B. (1963). *J. Appl. Physiol., 18,* 619.

Åstrand, P.-O. and Saltin, B. (1964). *J. Appl. Physiol., 19,* 829.

Beaumont, W. van and Bullard, R. W. (1963). *Science, 141,* 643.

Buskirk, E. R., Iampietro, P. F. and Bass, D. E. (1958). *J. Appl. Physiol., 12,* 189.

Craig, F. N. and Cummings, E. G. (1966). *J. Appl. Physiol., 21,* 670.

Darrow, D. C. and Yannet, H. (1935). *J. Clin. Invest., 14,* 266.

DeLanne, R., Barnes, J. R. and Brouha, L. (1958). *J. Appl. Physiol., 13,* 97.

Eichna, L. W., Bean, W. B., Ashe, W. F. and Nelson, N. (1945). *Bull. Johns Hopkins Hosp., 76,* 25.

Greene, C. H. and Rowntree, L. G. (1927). *Am. J. Physiol., 80,* 209.

Greenleaf, J. E. (1966 *a*). *National Aeronautics and Space Administration Special Publication 110.*

— (1966 *b*). *Int. J. Biometerol.* In press.

Greenleaf, J. E., Averkin, E. G. and Sargent, F. II. (1966 *c*). *J. Appl. Physiol., 21,* 93.

Greenleaf, J. E., Matter, M., Jr., Bosco, J. S., Douglas, L. G. and Averkin, E. G. (1966 *d*). *Aerospace Med., 37,* 34.

Greenleaf, J. E., Prange, E. M. and Aver-

KIN, E. G. (1967). *J. Appl. Physiol.* In press.
GREENLEAF, J. E. and SARGENT, F. II (1965). *J. Appl. Physiol., 20,* 719.
HABENER, J. F., DASHE, A. M. and SOLOMON, D. H. (1964). *J. Appl. Physiol., 19,* 134.
HARDY, J. D. and DRABKIN, D. L. (1952). *J.A.M.A., 149,* 1113.
HENSCHEL, A., TAYLOR, H. L. and KEYS, A. (1953). *J. Appl. Physiol., 6,* 624.
HUNT, E. H. (1912). *J. Hyg., 12,* 479.
ILZHÖFER, H. and BRACK, H. (1932). *Arch. f. Hyg., 109,* 20.
JAROŠOVÁ, V. and DAUM, S. (1951). *Čas. Lék. Česk., 90,* 1014.
JUDY, W. V. and GREENLEAF, J. E. (1966). *Aerospace Med., 37,* 285.
KALTREIDER, N. L. and MENEELY, G. R. (1940). *J. Clin. Invest., 19,* 627.
KEYS, A. and TAYLOR, H. (1935). *J. Biol. Chem., 109,* 55.
KJELLMER, I. (1961). *Med. Exp., 5,* 56.
KOZLOWSKI, S. and SALTIN, B. (1964). *J. Appl. Physiol., 19,* 1119.
KRONFELD, D. S., MACFARLANE, W. V., HARVEY, N., HOWARD, B. and ROBINSON, K. W. (1958). *J. Appl. Physiol., 13,* 425.
KUNO, Y. (1956). *Human Perspiration.* Springfield, Illinois: Thomas, pp. 251–276.
LADELL, W. S. S. (1955). *J. Physiol., 127,* 11.
LAVIETES, P. H., D'ESOPO, L. M. and HARRISON, H. E. (1935). *J. Clin. Invest., 14,* 251.
MOORE, R. and BUSKIRK, E. R. (1960). Exercise and Body Fluids. In: *Science and Medicine of Exercise and Sports.* Edited by W. R. Johnson. New York: Harper, pp. 207–235.
PITTS, G. C., JOHNSON, R. E. and CONSOLAZIO, F. C. (1944). *Am. J. Physiol., 142,* 253.
ROBINSON, S. (1963). Circulatory Adjustments of Men in Hot Environments. In: *Temperature, its Measurement and Control in Science and Industry.* Vol. 3, Part 3: Biology and Medicine. Edited by J. D. Hardy. New York: Reinhold, pp. 287–297.
ROTHSTEIN, A., ADOLPH, E. F. and WILLS, J. H. (1947). Voluntary Dehydration. In: *Physiology of Man in the Desert.* Edited by E. F. Adolph. New York: Interscience, pp. 254–270.
SALTIN, B. (1964 *a*). *J. Appl. Physiol., 19,* 1114.
— (1964 *b*). *J. Appl. Physiol., 19,* 1125.
— (1964 *c*). *Acta Physiol. Scand., 62,* Suppl. *230,* 1.
SALTIN, B. and STENBERG, J. (1964). *J. Appl. Physiol., 19,* 833.
SCHLOERB, P. R., FRIIS-HANSEN, B. J., EDELMAN, I. S., SOLOMON, A. K. and MOORE, F. D. (1950). *J. Clin. Invest., 29,* 1296.
SMITH, J. H., ROBINSON, S. and PEARCY, M. (1952). *J. Appl. Physiol., 4,* 659.
VERNON, H. M. and WARNER, C. G. (1932). *J. Hyg., 32,* 431.
WESSON, L. G., JR. (1960). Kidney Function in Exercise. In: *Science and Medicine of Exercise and Sports.* Edited by W. R. Johnson. New York: Harper, pp. 270–284.
WOLF, A. V. (1958). *Thirst. Physiology of the Urge to Drink and Problems of Water Lack.* Springfield, Illinois: Thomas.

DISCUSSION

Kraut: G. Lehman of the Max-Planck-Institut für Arbeitsphysiologie investigated the fluid composition of trained hot-plant workers in a glass factory. He found that the well-trained workers lose less sweat than the untrained ones. During the shift, they drink fluid often but in very small amounts, with the result that the osmolarity of the blood plasma is maintained. Only $^1/_3$ to $^2/_5$ of the fluid loss is replaced. The rest must be taken after the shift, in order to be fit at the beginning of the next shift.

Mašek: Just to confirm the observations of Prof. Kraut and Dr. Greenleaf, I would like to add two observations made at our Institute some 12 years ago in hot-plant workers. The untrained ones drank excessively at first, very little later. The same phenomenon could be repeated in rats, when a cold draught led to quick repletion with water. *Lát,* who made these experiments, expressed the hypothesis of hyperexcitation of the cutaneous receptors, producing suppression of appetite and thirst in the central nervous system, which could be eliminated by a cold-air draught.